THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[THIRD SERIES.]

No. 12. DECEMBER 1858.

XL.—*On the Cambium-layer of the Stem of the Phanerogamia, and on its Relation to the Increase of Thickness.* By H. von Mohl*.

During the last twenty or thirty years, investigations on the development of the stem have led to the discovery that, in spite of the great difference of structure in the stems of the Monocotyledons and Dicotyledons, the course of their development presents a far greater agreement than was formerly imagined. Satisfactory as this progress is on the one hand, yet, on the other, labourers in this field have, at least so it appears to me, promulgated many erroneous theories; hence a discussion of this subject will not be inopportune.

It will be most convenient to recur, in the first place, to Schleiden's works. In his explanation of the peculiarities of vegetable tissues †, he assumed the existence of three stages of cell-development in the earliest period. In the first stage, the new products present themselves in the form of an *apparently* structureless, yellow, pultaceous mass; in the second stage, in which the process of cell-formation has just ceased, there is a distinct delicate cellular tissue with more homogeneous contents, which, however, is still completely saturated with sap; in the third stage, the cellular tissue assumes a blackish appearance, arising from the fact that all the intercellular passages are then emptied of sap and contain only air.

According to Schleiden's view, the arrangement of the cellular tissue influences the conformation of the stem exclusively in the first stage. This depends—1. on the *arrangement of the*

* Translated from the 'Bot. Zeitung,' xvi. p. 184 *et seq.*, June 25 and July 2, 1858, by Arthur Henfrey, F.R.S., &c.

† Grundz. d. wiss. Bot. 1843, ii. 127.

secondary cells in the parent-cells, so that a linear disposition of the secondary cells in the parent-cells in the long axis of the stem lays the foundation of an elongated internode—an arrangement agreeing with the angles of a tetrahedron (*sic*?), of an undeveloped internode—and an arrangement in a plane standing perpendicularly to the axis forms an internode greatly developed in breadth; 2ndly, on the *form of the process* itself, this ceasing at certain places sooner than in others.

In the second stage of the process of cell-development, the general uniform expansion of the cells formed in the previous stage can alone act; in this period, therefore, the volume may alter, but not the form and relations.

In the third stage, the expansion of the existing cells is the exclusive influence in determining form.

This distinction of three stages is retained in the later editions of the same work (3rd ed. ii. p. 132), and the cambium (*cambial layer, formative layer,* p. 153) is specially defined as a cellular tissue which has not yet ceased to form new cells, which, according to the passages above referred to, would be limited to the first stage.

It will not be superfluous, before going further, to examine this conception of the cambium a little in detail. I leave out of the question the circumstance that examination made with any care shows that the youngest cellular tissue never forms an even apparently homogeneous pultaceous mass, but that its composition of cells is always clearly perceptible—so that the observer can find no distinction between the first and second stages; and the further circumstances, that the cells of vegetative organs are multiplied by division, and not by free-cell-formation, and that the intercellular passages do not become visible in consequence of the fluid contained in them being replaced by air, but from the cells, which in the cambium-layer are connected together as far as their extreme angles, subsequently separating from each other at the angles, which become rounded-off. A more important circumstance is, that the multiplication of cells occurs not merely in the period which Schleiden calls the first stage, but also in the second, and very often in the third: consequently, that division into stages, attempted by Schleiden, cannot be carried out; and the assertion that all elementary organs originate in the first stage of cell-development of an organ, and that the subsequent development of the latter depends simply upon growth of the cells, is decidedly incorrect.

I believe that, in the examination of a young organ, we may distinguish three stages of cell-development; but these must be differently defined. The youngest and most rudimentary parts are composed of parenchymatous cells closely applied together and forming a uniform tissue, in which we can find no trace of the subsequent separation into parenchyma, vascular bundles, &c. We may term this, with Schacht, the *primary parenchyma* (*Urparenchyma*): the restriction of the term *cambium* to this tissue would be very appropriate, were it not that this name has long been generally applied to the structures of the second period, and especially to the still more developed cambium-layer of Dicotyledonous trees. In the second period the tissue separates into the different classes of tissues, the formation of parenchymatous cells being continued by the division of a portion of the cells in different directions of space; while in other groups of cells the formation of elongated cells, vessels, &c., results from the predominance of longitudinal division, and the omission, or rare occurrence, of cross-division. In this period also the tissue has very delicate cell-walls, and, from the absence of intercellular passages, is still transparent. The cell-walls of this and the preceding period have the peculiarity, in contrast to the walls of more developed cells, that they attract the pigment from a solution of carmine, and become tinged bright red. The commencement of the third period, in which the tissue emerges from the condition of cambium, is marked in the parenchyma by the appearance of intercellular passages, which become filled with air, and in the elongated cells, vascular tubes, &c., by the deposition of secondary layers. The longitudinal division of the parenchymatous cells in the direction parallel with the surface of the axis has now pretty well ceased; but the transverse division and the multiplication of cells lengthwise of the axis lasts for a considerable time longer in many cases. This allows the possibility of particular parts of a tissue, thus tolerably advanced in development, and even arrived at complete conformation, recurring again to the condition of cambium, producing within them a young tissue by cell-division, thus giving rise to the formation of vascular bundles, peridermal layers, &c.

Passing from the consideration of the cambium to Schleiden's account of the development of the stem, the following five cases are described*.

A. The first distinction occurs between Monocotyledons and Dicotyledons, in the latter of which the individual vascular bundles continually increase in thickness, while in the Monocotyledons this process of cell-formation ceases from below upwards, and hence thickening of the individual internodes becomes impossible, and a thickening of the axis can only arise successively from the following internodes becoming constantly broader.

The *Dracænæ*, indeed, form an exception to this.

* Grundzüge, 1st ed. ii. p. 128.

B. If the formative process advances regularly from below upwards, a definite plane of the base ceasing to form cells, a cylindrical ascending axis is formed. This process occurs in stems with elongated internodes.

C. If the process of cell-formation ceases at particular parts of the periphery earlier than at others, the result is an axis with projecting ridges, trigonous, &c.

D. If the cell-formation lasts longer at the circumference than in the middle, and the terminal bud is of the usual conical form, the cell-formation occurs, not in the whole cone, but only in a superficial region, forming a kind of conical cap or mantle on the cone (*Kegelmantel*), so that the whole free surface of the cone contains the younger cells, the central part of the cone the older. Here the whole axis of the cone ordinarily rises cylindrically upwards; but not by similar superposed disks (as in B), but by superposed hollow cones (*Kegelmantel*). Each new internode is a hollow cone of this kind, and therefore cannot be cut off by a section perpendicular to the axis, but only by a cut following the surface of the cone. If the process of cell-formation lasts somewhat longer in the later internodes than in the earlier, a more elongated hollow cone is formed, which consequently projects over the base of its predecessor, which would otherwise be free, and the new internode becomes broader in proportion to the older (in *Melocactus, Zea,* &c.).

E. If the cell-formation ceases earlier at the margin than in the middle, and the new cells formed in the middle arrange themselves successively in planes, the margin must rise up, the middle becoming gradually developed into a hollow form, just as a disk of lead becomes concave when it is hammered in the middle and not at the edges. In this way is produced the funnel-shaped end of the stem of *Echinocactus,* the calyx of *Rosa,* &c.

In another place (ii. p. 147) Schleiden gives the following explanation of the variation of the internal organization of stems, in which he sets out from the idea that, as the cellular tissue is formed, a portion of it is always changed into vascular bundles; consequently the direction of the vascular bundles depends wholly upon the direction of the formative energy. On this account, in long-jointed stems, where the cell-development takes place from below upwards, as it were, in horizontal disks, the vascular bundles are straight and tolerably parallel to the axis of the stem; where, on the other hand, one hollow cone is superposed on another in the terminal shoot, the vascular bundles take, in their first formation, a course from the base of the cone to its summit, therefore from the circumference of the internode to its axis; and subsequently, when new internodes are superadded, the vascular bundles of the first hollow cone are developed on through the following, as far as the circumference, where they enter leaves or buds. They therefore form an arc convex internally, the length and convexity of which depend upon the form of the terminal bud.

Since all the new portions, whether these be in the form of thickenings of the old vascular bundles in the Dicotyledons, or the rudiments of new vascular bundles in the Monocotyledons, are constantly formed on the outside of the primary vascular bundles, the older and deeper-seated bundles running from the axis to the periphery of the leaves and buds must necessarily cross the younger bundles ascending higher in the axis, or the cambial structures which have been formed from within outwards.

In reviewing Schleiden's explanation of the development of the stem, we recognize above all, as the great merit of it, the statement that, as has long been known of the Dicotyledons, so also in the Monocotyledons, the origin of the vascular bundles occurs in a cambium-layer situated under the surface of the stem, in which is developed, simultaneously with the bundles, the parenchymatous tissue destined for the further completion of the stem. This explanation forms a strong contrast to the views of Meneghini, who believed that the vascular bundles were formed in the well-developed parenchymatous tissues through the influence of currents of sap. The correctness of the account given by Schleiden has been confirmed by all subsequent researches.

We cannot speak so favourably of the other parts of this theory, since Schleiden gives far too little weight to the diversities of internal organization corresponding to the systematic position of plants, and attributes far too much value to the external form of stems, especially to the length of their internodes, and ascribes their outward variations to internal differences of development which do not exist in nature.

That the Monocotyledons and Dicotyledons cannot be sharply separated from each other in respect to the internal structure of their stems—a series of intermediate structures existing—has long been known; yet, for all that, the distinction is very clearly marked in the great majority of cases. Schleiden only pays attention to the growth in thickness of the Dicotyledonous bundle, and the absence of this in the Monocotyledons. But this very point is well known to present many exceptions; it is therefore important to keep in view the second great distinction —the internal, convex, curved course of the vascular bundles of the Monocotyledons.

That I directed especial attention, in my 'Anatomy of Palms,' to this course of the vascular bundle, and to the difference of structure which one and the same bundle exhibits in different parts of its course, depended partly on the nature of the material at my disposal, which afforded me the means of studying the developed stems of a great number of Palms, but not the deep investigation of the history of development of the stem,—partly on the necessity of laying particular stress on this point, because it afforded the most striking evidence against the doctrine of the endogenous growth of the Monocotyledons, at that time universally received, and adopted by DeCandolle for the systematic division of the Phanerogamia. But even now the matter is not to be put aside so simply as is done by Schleiden; for this different course of the vascular bundles is a very characteristic mark of the Monocotyledonous stem, and the result of a peculiar mode of development.

In the majority of the Dicotyledons the young vascular bundles lie side by side in the cambium-layer, and ascend, without suffering any curvature towards the centre of the stem, up to the point where they turn outwards to the leaf; and the cambium-layer traverses in an uninterrupted circle the individual vascular bundles and the parenchymatous cells lying between them, so that the liber-layers of all the vascular bundles are situated outside the cambium-layer, in the bark. If new vascular bundles are formed, these are developed in the same cambium-cylinder which had given birth to the older vascular bundles, and between the latter. But since, in the interval between the formation of the older and younger vascular bundles, the former have been somewhat advanced in their development, and their woody portion thickened in the direction of the radius of the stem, the medullary cellular tissue of the stem having also grown outwards in like proportion, and the cambium-ring being thus forced outwards, the inner part of the wood of the younger bundles lies at a somewhat greater distance from the centre of the stem than the corresponding part of the older bundles, yet without the intermediate and outer parts of the new bundles being pushed further out than the older bundles.

In the Monocotyledons matters are essentially different. The vascular bundle formed by a direct transformation of a part of the cambium-layer lies, as in the Dicotyledons, in its whole length within the cambium-cylinder,—or rather, since the bud is always drawn to a point at the *punctum vegetationis*, within a hollow cone (*Kegelmantel*), forming a continuation of the cambium-cylinder. Simultaneously, and not only beside it but also on the peripheral side, parenchymatous cellular tissue is formed from the cambium, and through this the constantly renewed cambium-cone is moved outwards from the vascular bundle towards the circumference of the stem. This production of cellular tissue outside the vascular bundle is almost or quite at an end at that part of the stem where the lower end of the bundle lies, but increases more and more upwards; whence, in examining full-grown stems, the lower end of the individual vascular bundles are found at the outward boundary of the medullary parenchyma, and mostly covered only by a couple of layers of cells which belong to the latter tissue, while the upper part of the bundle, which at its origin is only separated from the centre of the stem by a small and no longer multiplying number of cells, and is subsequently covered on its outer side by thick layers of cells, is found deeply seated in the stem. The uppermost extremity, lastly, which already in the bud is connected with a leaf, in the further development of the bud must follow the leaf in proportion as this is pushed outwards from the centre towards the cylindrical periphery of the stem, and, in the same proportion as the cellular tissue is multiplied at the circumference of the stem, undergo an intercalary growth between the centre of the stem and the base of the leaf, and assume a more or less horizontal course from within outward. Since the same process is repeated in the cambium-cone pushed further out towards the periphery, the younger bundles, which originate in the expanded cambium-mantle, must run separate from the older, and further out in the stem. If, as is often the case in the Palms, both earlier- and later-formed bundles enter the same leaf, the place of the curvature into the leaf of the younger bundles will be found not so deeply seated in the full-grown stem as that of the older, because, at the time of their first development, the base of the leaf and the cambium-cone were already further removed from the centre of the stem, by the production of medullary cells, than at the formation of the older vascular bundles running into the same leaf. This condition was first made out and rightly explained by Meneghini.

Schleiden was well acquainted with this diverse mode of development of the Monocotyledonous and Dicotyledonous bundles; unfortunately, he adopted the notion that this was altogether independent of the circumstance whether the plant belonged to the Monocotyledons or Dicotyledons, but stood in connexion with the circumstance whether the internodes of a stem were elongated lengthwise into a cylinder, or remained abbreviated. In consequence of this, he fell from one error into another.

The mode of development of a cylindrical stem mentioned by him under B, in which the development progresses from below upwards in horizontal disks, whereby the vascular bundles acquire a straight direction and a position parallel with the axis, does not exist at all. Every stem, be its form what it may, terminates above in a *punctum vegetationis,* in which its leaves are formed, and towards which its youngest vascular bundles converge. This condition remains exactly the same, whether the apex of the stem be drawn out conically, flattened, or depressed. Whether the vascular bundles are all subsequently arranged in a cylinder under the rind, or whether, as in the Palms, they run inwards towards the centre of the stem, has nothing at all to do with the longer or shorter state of the internodes of the stem, but depends solely upon the difference above described, whether the cambium-cone continues to form parenchyma outside the vascular bundle or not. This does not take place in Dicotyledons with short internodes, as in *Sempervivum*, because it is not in accordance with the growth of Dicotyledons, while, on the other hand, it occurs in Monocotyledons with elongated internodes. The curved course of the vascular bundles of the latter from the leaf inwards to the centre of the stem, and from this, again, outwards and downwards to the periphery, was indeed discovered by me, in a hollow-stemmed Palm with long internodes. Schleiden is altogether incorrect (ed. 3. p. 158) in the detailed exposition of the proofs of the peculiar mode of vegetation which he ascribes to stems with long internodes,—that in them, for instance in the Grasses, the vascular bundles lying in one internode do not originate *seriatim* from within outwards, but are developed and perfected simultaneously. Examination of the terminal bud of a large Grass, for instance *Arundo Donax*, shows most distinctly, as indeed was already well known to Moldenhauer, that the outer vascular bundles originate much later, and occur in the still completely cambial condition while the inner already possess spiral vessels.

Just as little can we approve Schleiden's representation of the growth of stems with short internodes and a short bud-axis; for he here derives the vascular bundles, not from a common cambium-cone embracing the whole axis of the bud, but from a series of numerous successively-formed, funnel-shaped, hollow cones, stuck into one another, and with free margins. It is self-evident that this idea is decidedly incorrect, if applied to short-jointed Dicotyledonous stems, for instance to a fleshy *Euphorbia*, a *Sempervivum*, &c.: for the stems are constructed in every respect in the same way as the long-jointed; and it has no influence upon the mode of development of the individual internode and its vascular bundles, whether this grows in the longitudinal direction for some time after its emergence from the condition of a bud, by cell-development and expansion, or whether this process occurs only in a slight degree. We might be more inclined to countenance this notion in reference to the development of Monocotyledonous stems, since in these one cambium-cone is certainly formed over another; but the matter takes place in a different way from that described by Schleiden, and exactly in the same way as in a stem with cylindrical and elongated internodes, whose terminal bud is really just as conical as that of a short-jointed stem. The cambium-cylinder of a Dicotyledonous stem, which is constantly transformed on its inner side into woody layers and cells of medullary rays, and is constantly renewed on its outer side by development of cells, consists at different epochs of totally different cells, and occupies also a different place; but it remains always essentially the same, and no one would represent the matter by saying that in the course of time a more or less considerable number of distinct, concentric cambium-cylinders had been formed. Just as little ground, however, exists, if we do not admit this view, for regarding, with Schleiden, the development and renovation of the conical cambial mantle of the conical bud as the product of distinct and successive funnel-shaped cambial mantles, sticking into one another, with their edges free. The latter assumption rests upon a totally mistaken notion. Schleiden's view, that the bud possesses a distinct cambium-mantle in each internode, has no foundation in fact; one cambium-region is common to them all, and only its higher and lower zones correspond to the individual internodes. No trace exists of a free margin of a cambium-mantle belonging to a single internode; but the zone of cambium corresponding to each internode forms the immediate continuation of the cambium-zone of the next internode below, just as in cylindrical stems. When, with the advancing development of the bud in the upper portion of the cambium-mantle, the inner part is transformed into vascular bundles and parenchyma, and its outer part is renovated by development of cells, and in this way a new and more externally situated cambium-mantle is formed, this renovation occurs in a degree continually decreasing downwards to the place where the production of new cells entirely ceases, and the cambium-mantle passes into the now no longer productive cambial cylinder of the lower part of the stem. Hence the growing downwards of an upper cambium-mantle over the free margin of that belonging to a lower internode, in stems which are thicker above, is out of the question, since no such free margin exists. If a stem becomes thickened into an inverted cone, this arises from a greater number of elementary organs being developed in the upper internodes; but this does not generally take place suddenly, and it is not that an upper internode grows down over the periphery; for the lower internode takes part in the development of the upper, becoming inversely conical and passing gradually into the latter.

No less erroneous is the view that the cambium-cone corresponds to an internode, and that consequently the newly-formed vascular bundles run from the circumference of the internode to its axis, and subsequently, when new internodes are superadded, are developed onward through the new cambium-cones, to reach the buds and leaves. It is certainly conceivable that the vascular bundles might arrive at the middle of the stem already at the end of the first internode, and in the second internode run into the leaf, although no such stem has yet presented itself to me; but that would not alter the matter at all, and in such a bud there would be just as little correspondence of a special cambium-cone to each internode, as in a plant in which each vascular bundle runs through a dozen internodes.

Completely erroneous also is the idea that in short-jointed stems the internodes have a conical form corresponding to the form of the cambium-mantle, and stick into one another like funnels, so that they cannot be separated from one another by a horizontal section. A longitudinal section through the apex of a distinctly-jointed stem, for instance of *Arundo Donax*, shows that the internodes are not attenuated upwards, but that they are either separated from one another by horizontal planes, or are depressed downwards, so as to be concave.

This last condition leads me to the consideration of the form of stem spoken of by Schleiden under E, in which the bud is excavated in the middle. This not unfrequent depression of the point of the axis he believes to arise from the cell-formation ceasing sooner at the margins than in the middle, and that consequently the middle of the internodes assumes a hollow form, like a piece of metal plate when beaten out in the middle. This might happen if the internodes, like the metal plate, were free underneath; but as its under surface is continuous with the already more developed and more solid tissue of the subjacent internodes, a predominant development of cells in its centre would, to keep to Schleiden's comparison, no more render it hollow, than hammering a plate of metal, soldered to a block, would form it into a bowl. Cell-development predominant in the middle of the internode could only cause its expansion upwards, thus producing the opposite of what Schleiden expected. It is easily seen that such expansion of the *punctum vegetationis* is a consequence of just the opposite condition,—that the development of cells at the circumference is in excess, and the cells in the middle are further behind in their development—this stage being followed by a second period of growth, in which the cells of the centre extend longitudinally, whereby the meniscus form of the internodes is converted into a discoid, and the inwardly-curved surface of the stem is curved outwards and converted into a cylinder, as has been demonstrated most convincingly by Hofmeister in the depressed summits of the stems of Ferns.

Schleiden does not extend his researches (except in the case of *Dracæna*) to the examination of the question how the cambium-layer behaves in the stem after the unfolding of the bud, and what becomes of it in the full-grown stem, of the Monocotyledons. This point was taken up by Karsten ('Vegetationsorgane der Palmen,' 1847). This author had the great advantage, in his investigations made in the tropics, of possessing abundant material, consisting of living and entire plants,—an advantage which no one knows better how to value than myself, since, in my 'Anatomy of the Palms,' I was restricted for the most part to isolated fragments of stems.

Karsten explains most clearly how, in the terminal bud of the Monocotyledons, especially of the Palms, the wood-bundles take their origin in the cambial tissue of a hollow cone, the cambium of the latter becoming converted in some places into parenchyma, in others into the vascular-bundle tissue. With the progressive development of the bud into a stem, the hollow cone assumes at its lower end a cylindrical form. The increase of the cambium endures in it for some time, while its outer, and more particularly its inner surface, are simultaneously converted into parenchyma—certain portions of the cambial cells at the same time separating as it were from the parenchyma and becoming developed into the woody bundles running into the medulla, and in some plants also into the rind. After the various parts of the stem have thus been produced from the cambium-cone, the cell-producing energy is lost in the latter (except in the case of the *Dracænæ*), and the last remnants of the cambium undergo a transformation into a layer organized somewhat differently in different plants, which, in the full-grown stem, lies between the internal vascular bundles and the rind, and is termed by Karsten the wood-cylinder. In the Palms the cells of this wood-cylinder agree closely with the cells of the rind and of the medulla; and in this way originates a tissue, analogous to the medullary rays of the Dicotyledons, connecting the medulla and the rind. The same condition occurs in the Pandaneæ, Aroideæ, Orchideæ, and Grasses. In other plants the cells of the outermost layers of the cambium assume forms which differ essentially from those of the cells of the rind and medulla, especially by the great thickening of their walls (lignification), and form a boundary-layer between the medulla and rind, often consisting only of two strata of cells. The forms of these cells are varied: where the inferior terminations of the vascular bundles are connected together to form a reticulation, the cells are parenchymatous; where the vascular bundles have a parallel course, they are more or less prosenchymatous. The lignification of these cells induced Karsten to name the layer they form the woody layer (*Holzschicht*), without intending to indicate the import of the lignified tissue, as to whether its cells were wood-cells or liber-cells (p. 100). In *Dracæna* and allied plants, the cell-forming activity of the cambium is not exhausted by this conversion into lignified cells, but endures during the whole life of the stem, and gives rise to the production of woody layers, as in the Dicotyledons,—the bundles of which must not, however, be regarded as the inferior prolongations of the new vascular bundles formed above (p. 99), but may be compared with the annual rings of the Dicotyledons (p. 103).

In this interpretation of the boundary-line between medullary and cortical tissue, distinctly marked in many Monocotyledons, but altogether imperceptible in others, as a wood-cylinder, two questions arise:—whether this boundary-layer, composed of homogeneous cellular tissue, is to be compared with the fibrous layer of *Dracæna,* which is continually thickened throughout life; and whether this last structure corresponds to the annual rings of the Dicotyledons.

There is no doubt that the said boundary-line is formed in the Grasses, *Asparagus, Ruscus, Iris,* &c., in the following way: that in the cambium-layer, the further it is developed outwards, and the more the formation in it of vascular bundles approaches its close, the production of the medullary parenchyma-cells side by side with the bundles undergoes an alteration—the cells, as they come to lie more externally, becoming of smaller diameter and mostly of greater length, until the formation of new cells at last entirely ceases. In the first place, in spite of the outermost of these cells having far thicker walls and a much greater length than the inner medullary cells and the cells of the rind, they are no analogue of the wood, but merely a modification of the medullary parenchyma: and this is the more clear since the difference of length and thickness of the walls is by no means a constant character; for, as Karsten truly remarks, in the Palms this layer of cells cannot be distinguished from the cells of the medulla and rind. We find similar conditions recurring when we examine the corresponding region of the Dicotyledons. In trees we usually find the same condition as in Palms, the cellular tissue of their medullary rays passing into the cellular tissue of the bark without displaying essential variations in the organization of the cells; and the only distinction existing is, that at the limit between medulla and rind, the cells are capable of multiplying by division. In other Dicotyledons, on the contrary, we find a sharp line of demarcation between medullary and cortical parenchyma, similar to that in the rhizome of *Iris,* &c., and indeed with the same peculiarity, that the boundary-line lies a little outside the circle of vascular bundles, and the production of new cells in the boundary-layer is altogether at an end, as in the Monocotyledons. This is the case particularly in the stems of *Cucurbita, Cucumis, Lagenaria*, &c., also in the stems of *Basella alba* and *B. rubra*. Here also, as in the Monocotyledons, we find, instead of a cambium-layer connecting the cambium-regions of all the separate vascular bundles into a general closed cylinder, a defined external boundary to the medullary tissue, which undergoes no further alteration with time. How little indicative is the distinction between this structure of the stem and that of an uninterrupted passage from medulla into rind, is shown by the portions of the same stem situated below the cotyledons, where, in *Basella*, the boundary-region just referred to is certainly in some degree marked, by its cells being of somewhat less diameter than those of the rind and medulla, yet forming no definite boundary-line,—while in the cotyledonary internode of the Cucurbitaceæ mentioned above, the cellular tissue of the rind and medulla is of quite uniform structure, and no trace can be found of any line of demarcation between them. Under these circumstances, it does not seem warrantable to apply to the peripheral region of the medullary parenchyma, formed last out of the cambium of the Monocotyledons, the term 'wood-cylinder,' since (not to dwell upon the vessels in this situation) a portion of the stem to which the name of wood should apply, ought to present at least a decided contrast to the parenchyma of the stem; here, however, such a contrast either has no existence, or depends on mere thickening of the walls of parenchymatous cells, or upon a slight alteration of form (elongation) of the medullary cells, which takes place with a gradual transition. These boundary-cells are structures of arrest or limitation (*Hemmungsbildung*), with which the medullary cells cease their reproduction on the outer side.

The case is different in *Dracæna*. Here the formation of new tissue does not cease; the product of the continuously developed cambium-layer, however, does not consist of mere parenchyma-cells, but, as in the antecedent formation of the vascular bundles, of two kinds of tissue—parenchyma-cells and fibrous bundles. Here there exists a clear analogy to the normal formation of the wood of Monocotyledons, although the bundles are imperfect, containing no vessels. In accordance with the type of the Monocotyledonous stem, the new layers of wood are not formed in continuous concentric layers, but in the form of isolated, although freely anastomosing, bundles. If, with Karsten, we apply the name wood-cylinder to these external bundles, the essential difference of their organization is a reason for not extending the name to the boundary-layer of the other Monocotyledons consisting simply of cellular tissue; for in the latter the formative energy of the cambium is lost before it arrives at a condition to form the wood-cylinder. In my 'Anatomy of Palms,' I took these outer vascular bundles of *Dracæna* for the lower ends of the bundles belonging to the leaves above, and Unger* was led by his investigations to agree with this; but I now think that Karsten was right in stating this view to be erroneous. The comparison made by Karsten (p. 103) between these outer bundles and the annual rings of the Dicotyledons is less admissible, since the latter, especially in our native trees, owe their origin chiefly to the further development of the cambium situated upon the individual primary vascular bundles between the wood and the liber, and therefore are of essentially different derivation from the outer vascular bundles of the *Dracænæ*. More satisfactory would be the comparison of these vascular bundles with those layers of wood which, in many Dicotyledons with widely diffused bundles, as in the Balsamineæ, are developed from that part of the cambium-layer which lies between the primary vascular bundles; and still more apt is the comparison with those external woody bundles of the Nyctagineæ, Chenopodeæ, &c., sometimes arranged in concentric circles, and sometimes confounded into more or less irregularly arranged masses, which Unger has so beautifully investigated, and which, in like manner, have no relations with the leaves. Doubtless many analogies might be made out between the organization of the stem of the *Dracænæ* and that of the stems of many tropical climbers; but as I have no opportunity myself of following out the development of the latter forms, I shall not enter upon this point. The outer bundles of the *Dracænæ* contain no vessels, their elementary organs corresponding rather with those of which the liber-bundles of the Monocotyledons are composed. Hence it may appear doubtful whether they are comparable at all with the vascular bundles; but this objection appears of small weight when we bear in mind that the same anatomical characters are frequently found in the lower portions of all the vascular bundles of Monocotyledonous plants. In fact, this circumstance was one of the reasons for my regarding these bundles as the inferior prolongations of those bundles passing out into the leaves higher up in the stem.

Schacht attempted to extend the theory of the cambium-ring and its development into wood by setting up a series of special laws (while he coincided in general with Karsten's views), in obedience to which the development of the different portions of the stem should take place. Whether his attempt was a fortunate one, will appear from the sequel.

One of the most general of these laws ('Pflanzenzelle,' p. 255)

* Bau u. Wachsthum d. Dikot. Stammes, p. 37.

asserts that the vascular bundles originate in the primary parenchyma (*Urparenchyma*) of the embryo, and increase in number solely by ramification, and that no new independent vascular bundles can be formed in the plant.

The dogma thus generally expressed is decidedly erroneous. We may admit it for the vascular bundles belonging to one axis, originating by the development of a common connected cambium-sheath: for no one now entertains any doubt of the want of foundation of the view of Du Petit Thouars and his followers, that the vascular bundles originate in the leaves and run down in the stem to the points of the roots; for the vascular bundles entering the leaves from the stem are developed from below upwards. But it is another question, and, as it appears to me, one not yet solved by existing researches, whether in all plants the primary vascular bundles lying at the circumference of the pith are connected together, or whether there do not exist plants in which the young vascular bundles which run to leaves situated higher up, are formed between the older, without entering into connexion with them, and whether the mutual connexion of them is not effected by the subsequently produced woody layers. We shall, however, leave this point out of consideration.

On the other hand, there can be no doubt that the roots of Monocotyledonous stems possess their own bundles, which only subsequently enter into connexion with the vascular bundles of the stem, and (at least in many cases) cannot be derived from the same cambium-layer which was the place of origin of the latter. The Palms and Pandaneæ are the most favourable plants for the investigation of these conditions. In the former, the observations of myself, Mirbel, and Karsten agree that the roots originate under the rind, in that layer of the stem through which the most external fibrous bundles run—therefore in a layer where, in a fully developed Palm-stem, no peripheral cambium-layer any longer exists. Here there is formed locally for each root a nucleus of new cambium-tissue, by the transformation of parenchyma-cells existing long before; and in these nuclei originate the vascular bundles, which on the one side grow forward with the roots and form the wood of the roots, well known to be very different from the vascular bundles of the stem,—on the other side spreading out like a tuft, and penetrating an inch deep into the parenchyma of the stem, become entangled with the vascular bundles of the stem, and apply their extremities upon them. One must of course give up any idea that these vascular bundles grow into the cellular tissue of the stem in the manner of a root growing into the earth; they can only be formed by the transformation of particular portions of the parenchyma of the stem into cambial tissue, and the development of the latter into vascular bundles. But they are decidedly new structures, and not prolongations or ramifications of the vascular bundles of the stem.

The branches of the roots of the Monocotyledons stand in the same relation to the roots as the latter do to the stem, since they are developed outside a cambium-cylinder which has ceased to develope, and their ramifications penetrate backwards between the vascular bundles of the root. Schacht (p. 101) denies that the roots of Monocotyledons produce new branches, if their cambium-cylinder is lignified early; but this is untrue, and he should have paid attention to what has been said on this subject by Karsten (p. 56), who was supported by totally different experience. The origin of the thick adventitious roots of *Pandanus* presents conditions analogous to that of the Palms; and Schacht (p. 320) is wrong in ascribing to their stems a continuously developed cambium-layer such as occurs in *Dracæna.*

Less evident, and, particularly in the Dicotyledons, less convincing on account of the presence of an active cambium-layer in which the adventitious roots originate, is the condition of the roots of herbaceous Monocotyledons and the radical branches and adventitious roots of the Dicotyledons, in which the earliest vessels belonging to the root appear in the form of a wreath of vessels, and lie upon the lateral surfaces of the subjacent vascular bundles; but Trécul* was right in regarding the circumstance that these vessels are not continuous with the vessels of the stem or of the roots from which the new roots arise, as a proof that the adventitious roots possess vessels of their own.

With regard to adventitious buds, also, it may be proved that they form their own system of vascular bundles. The evidence is indeed not striking in the common cases where the adventitious buds form in the cambium-layer of the Dicotyledons, on which account I shall not dwell upon this subject, so well investigated by Trécul (*l. c.* p. 268). Perfect proof can only be afforded by those adventitious buds which originate in fully-developed cellular tissue at a distance from the cambium-layer of the parent plant, in which case there can be no doubt of the origin of their vascular bundles. Trécul (p. 280) observed one case of this in fragments of the roots of *Ailanthus,* in which adventitious roots had been formed outside the liber-layer: these stood in connexion with the cambium-layer of the stem by means of vessels which appeared to be younger than those contained in the bud. We cannot indeed attribute perfect conclusiveness to this observation, since it did not include the earlier stages of development, and only shows the probability, but not the certainty, of the independent development of the vascular bundles

* Ann. des Sc. Nat. 3 sér. viii. p. 290.

in the buds; but in the adventitious buds of *Begonia phyllomanica* it is beyond all doubt that the vascular bundles are dedeveloped quite independently of the cambium-layer of the stem. These buds originate in the outermost layer of the rind, and are separated from the cambium-layer by the entire, perfectly unaltered cellular tissue of the rind—at times, when they have already formed air-bearing spiral vessels in their axes and leaves.

The dogma that vascular bundles can only originate by the ramification of other vascular bundles, is therefore decidedly false.

Another axiom set forth by Schacht is, that only those vascular bundles whose cambium-layers coincide with the general cambium-layer of the stem can become thickened in the radial direction. Schacht on this account applies to the cambium-layer the name of thickening-ring (*Verdickungsring*), and attributes the incapacity of the Monocotyledons to increase in thickness to the want of this coincidence.

This idea also I must declare to be erroneous. I mentioned above that in the stems of *Cucurbita*, *Cucumis*, &c., and *Basella*, the vascular bundles lie inside the medullary parenchyma; in young stems there is no trace of a cambium-ring connecting them; but this does not prevent the vascular bundles from growing very considerably in thickness, in the same manner as in other Dicotyledons. This would cause the rupture of the cellular tissue, comparable to medullary rays, lying between the vascular bundles, were it not that a secondary cambium-layer is formed, in consequence of this increasing thickness of the vascular bundles, by the division of the parenchymatous medullary cells between the latter, which renders possible the elongation outwards of the medullary rays. Here it is very evident that the vessels do not increase in thickness because they lie in a cambium-layer, but, on the contrary, a cambium-layer is subsequently formed on account of the thickening of the bundles.

A secondary cambium-layer may be formed not only in a direction parallel to the surface of the stem, but a similar phænomenon may occur in a transverse direction across the whole thickness of the stem, and then give rise to the formation of vascular bundles, which subsequently apply themselves to the bundles already formed from the cambial sheath of the stem. This occurs in the nodes containing a vascular plexus both of the Monocotyledons (for instance Grasses) and Dicotyledons (*e. g.* *Ricinus*). A longitudinal section through the terminal bud of these plants shows that these nodes originate at a relatively late period; for no indication of them can be found in the internal cellular tissue of the axis of the bud, and the medullary cellular tissue of the latter consists of uniform, recently-developed parenchyma. Some distance down only does it fall into transverse lamellæ, which are mostly convex downwards, and which, on account of the far more vigorous development of the intercellular passages containing air, appear alternately bright and dark, and of which the one set of strata corresponds to the future nodes and the other to the internodes. About this time the vascular bundles of the stem are developed in the cambium-sheath; and the cellular tissue of the medulla has lost the transparency of cambium, on account of the intercellular passages. Then only is formed, in the lamellæ corresponding to the nodes, a secondary cambium, in consequence of which the cambial tissue re-assumes its transparency; and in this cambium are developed the much-entangled vascular bundles which become interwoven with the vascular bundles of the stem.

Lastly, a third law enunciated by Schacht says that no new vascular bundles are formed in the cambium-ring of the Dicotyledons, but this is only in a condition to form parenchyma-cells, while the formation of wood-, liber-, and vascular-cells only proceeds from the cambium of the wood-bundles (p. 251). This axiom, which Schacht founded chiefly on the examination of the stem of *Urtica dioica*, is equally untenable with the foregoing. The ordinary organization of our native trees is even opposed to this. As is well known, the medullary rays run through the whole internode, longitudinally, between the vascular bundles in the young shoots of these, while the woody layers subsequently formed by the lateral ramification of the vascular bundles stand in connexion, and the medullary rings then only fill up the short meshes of the reticulation. This ramification of the vascular bundles running over the original medullary rays can only be brought about by a part of the cells of the medullary rays becoming transformed into wood-cells and vascular tubes, and converted into woody bundles, which, uniting with the product of the cambium-layer lying in the vascular bundles, form the connected secondary woody layers. But there are still more striking instances. I will not refer to the observations on tropical climbers made by others, since I cannot test them, and shall only call attention to one among the observations on this point made by Karsten (p. 140) on *Bannisteria nigrescens*, as this appears to me particularly convincing. In this, Karsten found that woody portions, presenting themselves in the form of rounded-off radii strongly projecting at the circumference of the wood, are not produced by the development of the primary vascular bundles, but consist of wood-bundles formed over the medullary rays. We may ascertain, even in plants which are at our disposal in a fresh state, that the medullary rays have the power to form woody bundles. This occurs in such plants as have the vascular bundles lying in the cambium-cylinder separated by very broad medullary rays. If we trace, for instance, the development of the stem of an *Impatiens,* we see that the cells of the medullary rays produced by the development of the cambium-ring become converted more and more into prosenchymatous cells, and that between them appear groups of vessels (but without spiral vessels), thus giving origin to new vascular bundles. Hartig* observed vascular bundles developed in the above-described secondary cambium-layer which appears in the medulla of *Cucurbita.*

XLI.—*On Additions to the Madeiran Coleoptera.* By T. Vernon Wollaston, M.A., F.L.S.

Fam. **Carabidæ.**

Genus Olisthopus, Dej.

Olisthopus humerosus, n. sp.

Olisthopus maderensis, var. β, Woll. Ins. Mad. 35 (1854).
—— *humerosus,* Schaum, in litt.

It is not without some little hesitation that I am induced to register the present insect as specifically distinct from the *O. maderensis,* of which I have hitherto regarded it as an insular modification (although certainly a very curious one) peculiar to the rocks of the Dezertas. And I may add that it is through the strongly expressed opinion of my friend Dr. Schaum of Berlin, who has stated his belief that the peculiarities which it exhibits are too great to be attributed to any combination of the local influences to which it may have been long exposed, that I now record it under the new trivial name which he has suggested, —a title indicative of a character about its shoulders, which are a trifle more produced (and angular) than those of the *O. maderensis.* The other points in which it recedes from its ally may be at once gathered by a reference to the 'Insecta Maderensia.'

Genus Stenolophus, Meg.

Stenolophus marginatus.

Stenolophus marginatus, Dej. Spéc. gén. des Col. iv. 427 (1829).
—— ——, Léon Fairm. Faun. Ent. Franç. i. 145 (1854).

Two Madeiran specimens of this insect have lately come under my notice; they were both captured near Funchal, one by Mr. M. Park, and the other by Mr. E. Leacock. The species

* Bot. Zeitung, 1854, p. 31.